

Trampling tolerance of understorey vegetation in different hemiboreal urban forest site types in Finland

Minna Malmivaara-Lämsä · Leena Hamberg ·
Irja Löfström · Ilkka Vanha-Majamaa · Jari Niemelä

Published online: 15 January 2008
© Springer Science + Business Media, LLC 2008

Abstract The effects of trampling on the understorey vegetation were studied in boreal urban forests of different fertility in the greater Helsinki area, Finland. The three studied forest types in decreasing order of fertility were: 1) herb-rich heath forest, 2) mesic heath forest, and 3) sub-xeric heath forest. We inventoried the cover percentages of understorey vegetation in 40 herb-rich, 75 mesic and 40 sub-xeric biotopes located in 51 urban forests varying in size (0.6–502 ha). Cover percentages were compared to those of untrampled reference areas. In our study, trampling tolerance increased with increasing fertility of the forest type. Wear of understorey vegetation correlated positively with the number of residents (i.e. recreational pressure) around the forest patch. In general, understorey vegetation cover in all three forest types was lower than in the same forest types in untrampled reference areas. Ground layer cover in urban forests was less than half of that in reference areas. Mosses, lichens, and dwarf shrubs, especially *Vaccinium vitis-idaea*, proved to be sensitive to trampling and consequently decreased in cover. The cover of tree saplings, mainly *Sorbus aucuparia*, and some resilient herbs increased.

Keywords Boreal forest vegetation · Recreational use · Trampling tolerance · Urban woodlands · Wear

Introduction

Forest fragmentation is increasing due to accelerating urbanisation, agricultural development, logging and road construction globally (Wade et al. 2003). In Finland, remnant forest plant communities are a common characteristic of urban landscapes. These small urban forest fragments have high numbers of recreational users, and thus, wear and tear of

M. Malmivaara-Lämsä (✉) · L. Hamberg · I. Löfström · I. Vanha-Majamaa
Finnish Forest Research Institute, P.O. Box 18, 01301 Vantaa, Finland
e-mail: minna.malmivaara@metla.fi

J. Niemelä
Department of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65,
00014 Helsinki, Finland

vegetation caused by trampling is considerable (Lehvävirta and Rita 2002, Malmivaara et al. 2002). In addition to trampling, there are several other anthropogenic factors, especially fragmentation and atmospheric input of nutrients, affecting urban forest vegetation. These cause eutrophication and floristic changes (e.g. Thimonier et al. 1992, Hamberg et al. 2008) and may also significantly affect the trampling tolerance of vegetation in urban areas.

The percentage cover, biomass or height of vegetation on trampled and untrampled areas are often recorded and compared to determine the trampling tolerance of vegetation (i.e. the ability of vegetation to withstand trampling) (see Liddle 1997). The proportion of vegetation remaining after trampling disturbance in relation to untrampled vegetation is used as a measure of trampling tolerance. Resistance (ability to withstand/resist damages caused by trampling) and resilience (ability to recover from trampling) of component plant species determine the trampling tolerance of different plant communities (Cole and Bayfield 1993, Cole 1995, Tolvanen et al. 2001). The growth form and the morphology of plant species have an effect on their resistance to trampling (Liddle 1997). Herbs with large and thin leaves found in fertile vegetation types as well as lichens of dry vegetation types low in fertility habitats, e.g. on rocky terrains, are fragile (Kellomäki and Saastamoinen 1975, Liddle 1997). Vegetation types with an understorey vegetation of low productivity are most easily damaged due to their slow rate of regeneration after disturbance (Kellomäki and Saastamoinen 1975, Cole 1987, Liddle 1997, Rydgren et al. 1998). They may take a long time; even hundreds of years, to recover from wear.

Several experimental studies compared the effects of manipulated short-term trampling on: different boreal forest types (Kellomäki and Saastamoinen 1975, Kellomäki 1977), subarctic plant communities (Tolvanen et al. 2001), mountain vegetation types (Cole 1987, 1995) and temperate plant communities (Littlemore and Barker 2003, Roovers et al. 2004). Kellomäki and Saastamoinen (1975) simulated short-term trampling by using a mechanical tamp. Their results showed that the relationship between the site fertility and the trampling tolerance of the understorey vegetation was curvilinear: the trampling tolerance of the vegetation on the poorest (*Cladonia* type) and the richest (herb-rich) sites was lower than that of the sites of medium fertility. However, the richest sites were more tolerant than the poorest. Kellomäki (1977) also found a curvilinear relationship between the site fertility and trampling tolerance of plant communities in his short-term pedestrian trampling experiment. Tolvanen et al. (2001), working in the subarctic subalpine Kilpisjärvi, indicated that the most fertile vegetation type, herb-rich birch forest, was more resistant to pedestrian trampling than less fertile vegetation types (*Vaccinium myrtillus* birch forest, *Empetrum nigrum* tundra and *Betula nana* tundra). Liddle (1975) also detected a close positive correlation between trampling tolerance and the productivity of the particular habitat.

Graminoids are considered to be more resistant to trampling than herbs and dwarf shrubs due to their caespitose or matted growth form (Cole 1995). They are also more resilient due to their fast rate of regeneration (Kellomäki 1973, Cole 1995, Tolvanen et al. 2001). Cole (1987) studied the effects of three seasons of experimental trampling on five montane forest communities and grassland in Western Montana, USA. He found sizeable differences among vegetation types in susceptibility to cover loss. *Festuca* grassland had the highest tolerance, ten times higher, than the most fragile forest types dominated by short shrubs and tall herbs. Cole (1995) concluded that tolerance was correlated more with resilience than resistance and that plants with perennating buds located above ground surface are less resilient than other plants.

Thus, it seems that when the fertility of the site type increases, at least to a certain point, the trampling tolerance of the understorey vegetation increases as well (Kellomäki and Saastamoinen 1975, Liddle 1975, 1997, Tolvanen et al. 2001). However, in long-term

trampling the expected order of forest types in respect to trampling tolerance might change (Kellomäki and Saastamoinen 1975). Tolvanen et al. (2001) suggested that long-term continuous trampling might change vegetation structure towards more tolerant, graminoid-dominated types.

We wanted to compare the effects of long-term continuous trampling on the understorey vegetation in urban forests of different fertility. These, mainly small forest fragments, have high number of recreational users and, thus, represent an ideal ‘experiment’ of trampling in nature. The knowledge about trampling tolerance of boreal forest types in urban areas is lacking, and this information is needed for the purposes of urban planning and management with the aim to preserve indigenous forest vegetation in urban areas.

Our aim was to determine 1) whether urban forests varying in fertility (herb-rich, mesic and sub-xeric) differ in trampling tolerance and, 2) the effects of trampling on the understorey vegetation species composition of these forest types. We hypothesised, based on the results of Kellomäki and Saastamoinen (1975), that trampling tolerance of the forest types studied would increase curvilinearly with increasing fertility; sub-xeric heath forest having lowest and mesic heath forest having highest trampling tolerance.

Materials and methods

Study sites and vegetation sampling

We selected 51 urban forest sites (0.6–502 ha in size) for the study. The study sites were located in the greater Helsinki area, southern Finland, in the hemiboreal vegetation zone (Ahti et al. 1968). Selected sites were biotope mapped based on understorey vegetation in the summers of 1998–2000. The three heath forest types studied were (in decreasing order of fertility): 1) herb-rich *Picea abies* and broad-leaved tree dominated *Oxalis acetosella*–*Vaccinium myrtillus* type (OMT), 2) mesic *Picea abies*, *Pinus sylvestris* and *Betula pendula* dominated *Vaccinium myrtillus* type (MT), and 3) sub-xeric *Pinus sylvestris* dominated *Vaccinium vitis-idaea* type (VT) (Cajander 1926). Altogether 40 OMT, 75 MT and 40 VT biotopes were sampled at different distances from the forest edge. The age of dominant trees was over 80 years and forest management practices had not been employed in these forests during the last five years. The topography of the sites was level. The dominant soil type was a podsol developed on moraine and the humus form was mor (VT, MT) or mull-like (OMT).

A 100 m² sized sample plot (or two if the biotope size was > 1 ha) was placed in the centre of each biotope for vegetation inventories. Within each sample plot, 1 m² sub-plots located 4 m in the direction of all principal compass points from the centre point of the sample plot were used in the understorey vegetation inventories. All understorey vegetation species, including tree saplings under 50 cm in height, with the exception of liverworts and lichens were determined to the species level. The cover of plant species and litter on the sub-plots were estimated visually by using a scale of 0.25–100% with cover values above 10 % estimated in 5% intervals: 0.25, 0.5, 1, 2, 3, 5, 10, 15, 20 ... 90, 95, 100. The mean values of the cover percentages for the four sub-plots per sample plot were used in the statistical analyses. The nomenclature here follows Hämet-Ahti et al. (1998) for vascular plants and Koponen (1994) for mosses.

In addition, we measured basal area, volume and the number of stems per ha of coniferous and broad-leaved trees (> 5 cm in dbh) and the cover of shrubs and tree saplings (> 50 cm in height and < 5 in dbh) in each 100 m² sample plot and used them as measures of tree density and tree species composition in analysing our data (see below).

We used the total area of paths within the 100 m² sample plots as an estimate of trampling, and distance from the forest edge as a measure of fragmentation (edge effects). In addition, as measures of recreational use, data on the number of residents within the distance of 1 km and children in schools and kindergartens within the distance of 300 m from the centre points of the sample plots were collected from resident registers. The forest types studied did not differ in any biased manner in the ranges of the area of paths, the number of residents, the number of children in schools and kindergartens, the size of forest area and the distance from the forest edge (Table 1). Thus, the forest types were similar enough for trampling tolerance and species composition comparisons.

Statistical analyses

Because there were characteristic differences in OMT, MT and VT field and ground layer vegetation (Kuusipalo 1996, Tonteri et al. 2005, see Fig. 1; our data), we used relative understorey vegetation cover (urban/reference ratio) in comparing the trampling tolerance of the forest types. The urban/reference ratio reflects wear of the urban understorey vegetation compared to vegetation in untrampled reference areas. A value < 1 indicates the wear of understorey vegetation; the smaller the value the more worn the vegetation. We also compared the urban understorey vegetation data (cover percentages estimated in the field) to the data from untrampled reference areas to study the effects of trampling on the vegetation composition of each forest type.

The reference data of the same forest types (OMT, MT, VT) and of the same age (ca. 80 years) was collected from commercial forests of hemiboreal vegetation zone in southern Finland during the Eighth National Forest Inventory in 1985 (Finnish Forest Research Institute, unpublished data). Commercial forests were used as a reference because it was impossible to find suitable untrampled patches in urban forests. The major difference between urban forests and reference areas used here is the number of residents in the surroundings, which strongly correlates with the amount of recreational use and the concomitant wear of urban forest understorey vegetation (see Malmivaara et al. 2002). Effects of other factors possibly differentiating urban forests from reference areas and affecting understorey vegetation, such as fragmentation and related atmospheric deposition of pollutants and nutrients at forest edges, have been controlled in the analysis (see below) and are discussed in this paper.

Table 1 Minimum, maximum and mean values of selected environmental variables in OMT, MT and VT urban forests

Variable	OMT (<i>n</i> =40)		MT (<i>n</i> =75)		VT (<i>n</i> =40)	
	Min–Max	Mean (SD)	Min–Max	Mean (SD)	Min–Max	Mean (SD)
Path area (m ²)	0.0–37.8	6.1 (8.7)	0.0–40.8	4.8 (8.1)	0.0–99.5	12.4 (25.6)
Residents 1 km	360–16,320	8,104.5 (3,682.0)	154–16,317	6,556.6 (3,671.1)	44–17,200	6,636.5 (5,196.9)
Children	0–1,325	261.6 (447.7)	0–1,325	161.7 (343.0)	0–949	156.8 (270.0)
Forest size (ha)	1.4–339.0	36.5 (59.7)	0.6–339.0	47.6 (66.8)	0.6–502.0	49.2 (95.0)
Edge distance (m)	8–363	50.9 (75.5)	8–388	67.9 (74.2)	10–310	73.5 (69.9)

ANOVA or Kruskal–Wallis test were used in comparing the forest types. There were not statistically significant ($p < 0.05$) differences between mean values of the forest types

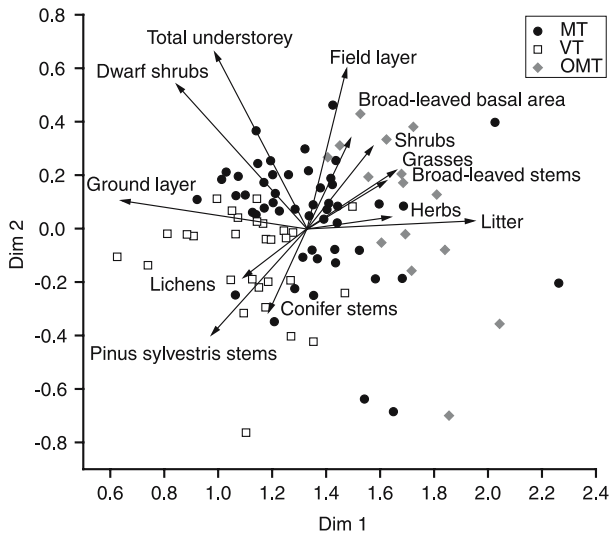


Fig. 1 Global Non-Metric Multi-Dimensional Scaling (GNMDS) describing the understory vegetation of OMT, MT and VT urban forests. A clear gradient from sub-xeric conifer and dwarf shrubs dominated vegetation of VT via mesic MT vegetation to broad-leaved tree dominated herb-rich OMT vegetation can be seen. Understorey vegetation of biotopes next to each other in the ordination space are more similar than of those far apart from each other. Variables describing vegetation structure with maximum correlations over 0.30 are presented as vectors. Arrows are showing the direction of increase in the variables. The length of each vector indicates the strength of the correlation with the ordination configuration

A Generalized Additive Mixed Model (GAMM) was used to test our hypotheses concerning trampling tolerances of the forest types and to quantify the effects of factors thought to affect the cover of understory vegetation in urban forests. Average values of model terms were used for predicting and drawing responses for understory vegetation cover of each forest type to increasing number of residents. All sample plots were included in this analysis ($n=155$). We used the R statistical software for the analysis (R Development Core Team 2005). The response variable (the relative understory vegetation cover, i.e., the urban/reference ratio) was modeled following the quasibinomial error distribution using the logit link function. We included one random factor (forest site) and seven fixed effect variables into the model as follows: 1) number of residents within a radius of 1 km, and 2) number of children in schools and kindergartens within a radius of 300 m (as measures of recreational use), 3) distance from the forest edge (as a measure of fragmentation (edge effects)), 4) total volume of trees > 5 cm in dbh (as a measure of tree density), 5) percentage of broad-leaved trees (as a measure of tree species composition/ ratio), 6) cover of litter, which has been shown to correlate negatively with the cover of mosses (Lahti and Väisänen 1987), and 7) forest type (as a measure of site fertility) as an ordered factor (OMT, MT, VT: ordered in the decreasing order of fertility). Forest size was not added into the model because of the strong positive correlation with the distance from the forest edge. Instead, we ran another model where distance from the forest edge was replaced by forest size. All fixed effect variables (except forest type) were smoothed as the responses of these variables were expected to be curvilinear.

We expected that the vegetation composition would be most altered within the first 20 meters from the forest edge where microclimate is usually drier and warmer than in forest interiors (Chen et al. 1993). Thus, to minimise the influence of forest edge on the vegetation

only biotopes ≥ 25 m from the forest edge were selected for species composition comparisons (18 OMT, 51 MT and 31 VT; $n=100$). We used either the t-test or nonparametric Mann–Whitney test when comparing vegetation composition between urban and reference forests.

Results

Trampling tolerance of understorey vegetation

Understorey vegetation was most worn in VT and least worn in OMT urban forests (Table 2, Fig. 2). The number of residents significantly affected ($p=0.03$) the relative cover of understorey vegetation. There was a strong positive relationship between number of residents and wear of understorey vegetation (Fig. 2): an increase of 15 000 residents within a radius of 1 km around a forest patch coincided with ca. 30% decrease in the relative understorey vegetation cover of each forest type. In addition, there was a significant effect of percentage of broad-leaved trees and litter cover on total understorey vegetation cover ($p \leq 0.002$). Understorey vegetation cover increased with increasing percentage of broad-leaved trees and decreased with increasing litter cover (Table 2, magnitude of responses not shown). The number of school and kindergarten children within a radius of 300 m from the centre point of the sample plot, distance from the forest edge, forest size (model not shown) and volume of all trees per ha did not significantly affect the understorey vegetation cover.

Understorey species composition

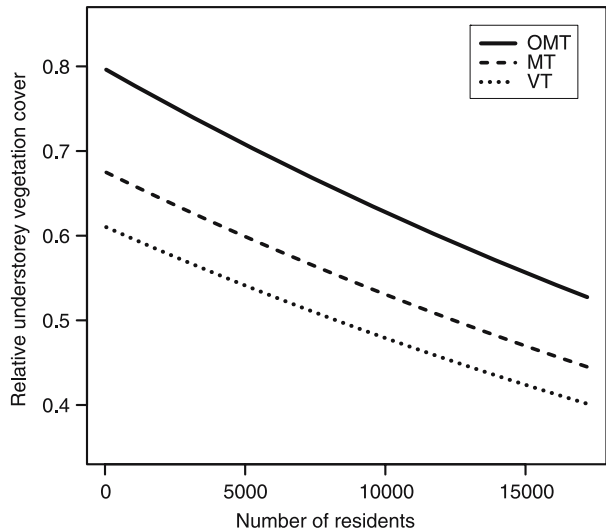
In urban forests, the total understorey vegetation cover in all three forest types was lower than in the corresponding reference areas (Table 3) as shown by the results of GAMM. The ground layer cover (mainly mosses) was only one fourth of that in OMT urban forests, and less than half of that in both MT and VT urban forests than in the same forest type reference areas. In the VT urban forests, the cover of the field layer was lower than in the VT reference areas. The cover of tree saplings (< 50 cm in height) in urban OMT and MT forests was ten times higher than in reference areas. The cover of shrub saplings was higher

Table 2 Generalized Additive Mixed Model for the relative understorey vegetation cover (Rel cover) used to describe wear of understorey vegetation

Model	R^2 (adj)	Intercept	Residents	Children	Edge dist	Tree vol	Broad —1%	Litter	Forest type L	Forest type Q		
($n=155$)		Coeff	P	P	P		P	P	Coeff	P	Coeff	P
Rel cover	0.347	-2.748	0.030	0.976	0.656	0.303	0.002	0.000	-0.295	0.000	0.039	0.426

Adjusted R^2 , coefficients of the terms not smoothed and p -values of all terms in the model are presented. Residents = the number of resident within a radius of 1 km, Children = number of children in schools and kindergartens within a radius of 300 m, Edge dist = distance from the nearest forest edge, Tree vol = volume of all trees >5 cm in dbh, Broad—1% = percentage of broad-leaved trees, Litter = percentage cover of litter, Forest type L = linear order of the forest type (Rel cover of OMT, MT, VT either in increasing or decreasing order); and Forest type Q = squared order of the forest types (Rel cover of OMT and VT higher or lower than that of MT)

Fig. 2 Relationship between relative understorey vegetation cover (urban/reference ratio), used to describe wear of understorey vegetation, and number of residents nearby ($p=0.03$) in OMT, MT and VT urban forests. A value <1 indicates wear of understorey vegetation; the smaller the value the more worn the vegetation. Predicted responses were drawn using average values of all GAMM terms (see Table 2) for each particular forest type



in urban than in reference OMTs. The cover of lichens and dwarf shrubs were lower and the cover of herbs higher in urban VT forests than in reference areas.

The cover of *Dicranum polysetum*, *Hylocomium splendens*, and *Pleurozium schreberi* mosses were considerably lower in urban forests than in reference areas (Table 4). On the contrary, the cover of *Brachythecium oedipodium* and *Pohlia nutans* were higher in all three urban forest types. For tree saplings, the cover of *Sorbus aucuparia* (in OMT, MT, VT) and *Picea abies* (in OMT) were higher in urban forests than in reference areas. The cover of the dwarf shrub *Vaccinium vitis-idaea* was lower in urban forests than in reference areas. For herb species, the cover of *Melampyrum pratense* was lower in urban OMTs and higher in urban VTs than in reference areas. *Pteridium aquilinum* was more abundant in urban than in reference OMTs, and *Trientalis europaea* was more abundant in urban than in reference MTs.

Tree layer characteristics

We compared tree layer characteristics in urban forests and reference areas and found that the upper canopy layers of urban OMT and MT forests were more open (i.e. stem densities were lower) than those of reference areas (Table 5). Furthermore, trees in urban VTs were larger than trees in reference VTs. Moreover, the cover of small broad-leaved trees (> 0.5 m in height and < 5 cm in dbh) was ca. 80% higher in urban forests than in reference areas.

Discussion

Trampling tolerance of understorey vegetation

Our results confirmed that the trampling tolerance of VT in comparison to the other two more fertile forest types is lower, which is consistent with the results of earlier studies (Kellomäki and Saastamoinen 1975, Liddle 1975, Tolvanen et al. 2001). OMT proved to be most tolerant of the three forest types, which was the opposite of our expectations based on

Table 3 Means of absolute understorey vegetation cover percentages in OMT, MT and VT urban forests (U) and in untrampled reference areas (R)

Cover percentage	OMT		<i>P</i>	MT		<i>P</i>	VT		<i>P</i>
	U (<i>n</i> =18) (SD)	R (<i>n</i> =20) (SD)		U (<i>n</i> =51) (SD)	R (<i>n</i> =36) (SD)		U (<i>n</i> =31) (SD)	R (<i>n</i> =18) (SD)	
Total understorey	64.3 (24.2)	94.4 (41.6)	0.011	70.9 (26.9)	113.3 (34.3)	0.000	60.4 (27.9)	112.5 (19.6)	0.000
Field layer	53.5 (24.4)	49.6 (27.9)	0.647	48.0 (21.4)	49.1 (27.9)	0.836	33.5 (16.8)	45.8 (19.3)	0.023
Ground layer	10.8 (9.7)	44.8 (31.9)	0.001	24.2 (19.2)	64.2 (25.2)	0.000	27.0 (19.8)	66.7 (17.4)	0.000
Grasses	11.4 (9.2)	15.3 (19.6)	0.792	7.0 (8.2)	9.2 (11.5)	0.626	5.3 (6.7)	8.2 (16.7)	0.669
Tree saplings	6.4 (6.5)	0.6 (0.5)	0.000	5.0 (7.8)	0.5 (0.8)	0.000	0.8 (1.2)	0.3 (0.5)	0.217
Shrub saplings	1.8 (3.1)	0.2 (0.8)	0.030	0.04 (0.2)	0.03 (0.1)	0.949	0.002 (0.01)	0.03 (0.1)	0.672
Dwarf shrubs	12.2 (9.3)	14.0 (13.4)	0.715	25.2 (15.3)	31.8 (19.5)	0.095	21.9 (12.2)	36.4 (23.0)	0.018
Herbs	15.9 (15.9)	19.6 (19.2)	0.430	7.0 (7.3)	7.6 (9.5)	0.491	4.4 (6.7)	0.8 (1.0)	0.031
Mosses	10.0 (9.2)	39.5 (30.5)	0.001	22.4 (18.0)	60.4 (25.5)	0.000	26.1 (19.9)	60.8 (18.6)	0.000
Liverworts	0.5 (1.3)	0.9 (3.1)	0.254	0.12 (0.3)	0.08 (0.2)	0.052	0.1 (0.1)	1.4 (3.6)	0.122
<i>Sphagnum</i> spp.	0.3 (1.2)	4.5 (11.5)	0.052	1.3 (4.2)	3.1 (10.2)	0.701	0.6 (3.2)	0.2 (0.6)	0.536
Lichens	0.02 (0.05)	0.03 (0.1)	0.908	0.02 (0.1)	0.6 (1.8)	0.095	0.1 (0.2)	4.2 (4.2)	0.000

T-test or Mann–Whitney test were used in comparing urban and reference forests. Statistically significant differences ($p < 0.05$) are indicated with boldface characters.

Total understorey = the cover of all field and ground layer species; Field layer = herbs, grasses, dwarf shrubs and tree and shrub saplings; Ground layer = mosses, liverworts, *Sphagnum* species and lichens; Grasses = all Poaceae species; Tree and shrub saplings = saplings < 50 cm in height (shrubs: *Corylus avellana*, *Rhamnus frangula*, *Ribes alpinum*, *R. nigrum*, *Rubus idaeus* and *Viburnum opulus*); Dwarf shrubs = *Vaccinium myrtillus*, *V. vitis-idaea*, *Calluna vulgaris*, *Empetrum nigrum* and *Arctostaphylos uva-ursi*; and Herbs = all herbaceous species

the findings of Kellomäki and Saastamoinen (1975). They suggested that the trampling tolerance of OMT might be lower than that of MT because of an abundance of sensitive herb species. However, our results demonstrated that the cover of total understorey vegetation was least worn in OMT urban forests.

The reason for the high trampling tolerance of OMT might be that the relative proportion of herbs, which are more resilient than dwarf shrubs (see Cole 1995), is higher than in MT and VT. Furthermore, regeneration after disturbance in OMT with highest productivity is fastest (see Cole 1987, Liddle 1997, Rydgren et al. 1998). Moreover, the nutrient load in urban areas may speed up the regeneration of OMT vegetation dominated by fast growing grass and herb species. Our results suggest that resilience rather than resistance of vegetation determines the tolerance of vegetation during a long-term trampling disturbance. This is in agreement with the results of Cole (1995).

Effects of recreational use on understorey vegetation

According to our results, the number of residents reflects the recreational pressure placed on vegetation. People tend to use forests near them on the daily basis in urban areas (see Jaatinen 1973, Sievänen 1987, Arnberger 2006). Children in particular use forests < 100 m from their homes (Florgård and Forsberg 2006). When the mean number of residents around a patch in our study (6500–8000) doubles (15000), the wear of understorey vegetation increases ca. 30%.

Table 4 Mean absolute covers of most abundant and/or frequent understorey vegetation species in OMT, MT and VT urban forests (U) and in the same site type untrampled reference areas (R)

Species	OMT		<i>P</i>	MT		<i>P</i>	VT		<i>P</i>
	U (<i>n</i> =18) (SD)	R (<i>n</i> =20) (SD)		U (<i>n</i> =51) (SD)	R (<i>n</i> =36) (SD)		U (<i>n</i> =31) (SD)	R (<i>n</i> =18) (SD)	
<i>Agrostis capillaris</i>	0.1 (0.3)	0.9 (3.9)	0.617	0.01 (0.04)	0.03 (0.1)	0.991	0.004 (0.02)	0.002 (0.01)	0.717
<i>Calamagrostis arundinacea</i>	7.9 (9.7)	6.6 (16.5)	0.374	2.5 (5.8)	4.3 (8.3)	0.107	0.2 (0.8)	0.2 (0.6)	0.701
<i>Deschampsia flexuosa</i>	1.3 (4.1)	3.4 (7.3)	0.064	3.4 (4.7)	3.9 (7.0)	0.431	4.3 (5.8)	7.6 (16.2)	0.668
<i>Melica nutans</i>	0.6 (1.5)	0.4 (0.7)	0.688	0.003 (0.02)	0.001 (0.01)	0.816	–	–	–
<i>Picea abies</i>	1.4 (4.2)	0.3 (0.4)	0.009	0.8 (2.9)	0.3 (0.8)	0.167	0.3 (1.0)	0.03 (0.1)	0.701
<i>Populus tremula</i>	0.9 (2.9)	0.02 (0.1)	0.120	0.1 (0.5)	–	–	0.002 (0.01)	0.001 (0.005)	0.717
<i>Sorbus aucuparia</i>	3.0 (2.9)	0.2 (0.2)	0.000	2.6 (3.7)	0.1 (0.3)	0.000	0.4 (0.7)	0.1 (0.2)	0.049
<i>Calluna vulgaris</i>	–	–	–	0.01 (0.1)	0.6 (1.7)	0.001	1.7 (3.0)	7.8 (11.7)	0.072
<i>Vaccinium myrtillus</i>	11.5 (9.2)	9.4 (10.4)	0.529	21.9 (14.3)	24.5 (16.6)	0.510	12.7 (9.8)	15.6 (18.8)	0.992
<i>Vaccinium vitis-idaea</i>	0.6 (0.9)	4.4 (5.7)	0.004	2.9 (3.2)	6.3 (6.9)	0.019	7.2 (5.8)	12.0 (9.1)	0.076
<i>Convallaria majalis</i>	5.2 (13.5)	0.02 (0.05)	0.112	0.3 (1.1)	0.1 (0.4)	0.253	0.1 (0.5)	0.04 (0.1)	0.600
<i>Linnaea borealis</i>	0.3 (0.6)	1.6 (4.3)	0.484	0.5 (1.2)	0.8 (1.6)	0.885	0.4 (1.0)	0.2 (0.6)	0.435
<i>Luzula pilosa</i>	0.6 (1.1)	0.5 (1.0)	0.757	0.9 (1.3)	0.4 (0.6)	0.068	0.6 (1.3)	0.3 (0.6)	0.888
<i>Maianthemum bifolium</i>	3.4 (3.6)	2.4 (2.7)	0.421	2.2 (2.4)	2.4 (4.3)	0.068	0.6 (1.2)	0.1 (0.3)	0.186
<i>Melampyrum pratense</i>	0.6 (1.1)	1.3 (6.0)	0.018	1.7 (3.4)	0.3 (0.6)	0.222	2.8 (4.4)	0.1 (0.2)	0.001
<i>Oxalis acetosella</i>	2.4 (3.3)	4.5 (11.4)	0.930	0.2 (0.9)	0.2 (0.6)	0.752	–	–	–
<i>Pteridium aquilinum</i>	5.0 (8.9)	0.4 (1.8)	0.031	3.4 (9.5)	1.8 (6.4)	0.189	1.0 (4.9)	–	–
<i>Trientalis europaea</i>	1.1 (2.5)	0.8 (1.4)	0.586	1.2 (2.2)	0.4 (0.8)	0.015	0.4 (0.7)	0.3 (0.8)	0.581
<i>Brachythecium oedipodium</i>	2.5 (6.0)	0.03 (0.1)	0.000	1.6 (2.5)	0.5 (2.9)	0.000	0.4 (0.8)	0.002 (0.007)	0.000
<i>Dicranum majus</i>	0.6 (2.0)	1.3 (3.4)	0.666	2.9 (6.2)	2.0 (6.0)	0.177	0.03 (0.1)	0.002 (0.01)	0.861
<i>Dicranum polysetum</i>	0.1 (0.2)	4.2 (11.1)	0.001	2.9 (4.2)	14.4 (15.4)	0.000	10.6 (13.9)	22.3 (13.4)	0.001
<i>Dicranum scoparium</i>	1.1 (3.0)	3.0 (6.2)	0.067	2.8 (3.5)	2.8 (4.4)	0.500	2.7 (2.8)	2.3 (5.4)	0.088
<i>Hylocomium splendens</i>	0.3 (1.2)	7.0 (11.0)	0.000	0.5 (1.4)	7.2 (8.1)	0.000	0.6 (1.9)	4.0 (5.8)	0.000
<i>Pleurozium schreberi</i>	1.2 (2.5)	19.6 (16.1)	0.000	8.3 (9.7)	28.8 (20.3)	0.000	10.3 (11.1)	29.7 (20.2)	0.000
<i>Pohlia nutans</i>	0.8 (2.1)	0.1 (0.3)	0.047	1.4 (3.1)	0.1 (0.1)	0.000	1.0 (1.4)	0.4 (0.9)	0.004
<i>Sphagnum angustifolium</i>	–	–	–	1.0 (3.9)	0.1 (0.5)	0.874	0.6 (3.1)	0.03 (0.1)	0.861

T-test or Mann–Whitney test were used in comparing urban and reference forests. Statistically significant differences ($p < 0.05$) are indicated with boldface characters

Table 5 Tree layer characteristics in OMT, MT and VT urban forests (U) and the same forest type reference areas (R)

Tree layer variable	OMT		<i>P</i>	MT		<i>P</i>	VT		<i>P</i>
	U (<i>n</i> =18) (SD)	R (<i>n</i> =20) (SD)		U (<i>n</i> =51) (SD)	R (<i>n</i> =36) (SD)		U (<i>n</i> =31) (SD)	R (<i>n</i> =18) (SD)	
Number of stems/ha	861.1 (480.4)	1149.8 (825.3)	0.202	680.4 (306.0)	908.7 (477.8)	0.008	754.8 (476.0)	842.1 (548.0)	0.561
Conifers	383.3 (295.6)	892.4 (836.5)	0.014	456.9 (269.3)	743.6 (442.2)	0.002	603.2 (299.4)	747.9 (530.9)	0.227
Broad-leaved	477.8 (528.7)	257.5 (301.0)	0.257	223.5 (292.3)	165.1 (207.2)	0.306	151.6 (317.1)	94.2 (167.6)	0.481
Basal area (m ² /ha)	31.7 (16.0)	26.8 (8.5)	0.188	27.2 (12.5)	22.5 (7.5)	0.121	27.5 (10.1)	19.0 (3.1)	0.000
Conifers	20.4 (18.1)	21.8 (10.2)	0.380	22.7 (14.2)	19.9 (8.8)	0.541	25.3 (8.5)	18.0 (3.2)	0.000
Broad-leaved	11.3 (14.1)	4.9 (7.7)	0.207	4.5 (6.1)	2.6 (3.7)	0.287	2.2 (4.4)	1.0 (1.4)	0.981
Shrubs (cover%)	13.8 (12.5)	5.3 (7.9)	0.016	10.2 (8.1)	5.2 (5.8)	0.002	6.2 (3.9)	3.6 (4.2)	0.032
Conifers	0.5 (1.4)	2.7 (3.9)	0.010	1.7 (2.7)	3.3 (4.2)	0.060	2.7 (3.1)	2.8 (3.8)	0.974
Broad-leaved	12.9 (12.9)	2.6 (6.4)	0.000	8.5 (7.1)	2.0 (3.6)	0.000	3.5 (3.2)	0.8 (1.1)	0.001

Number of stems and basal area of trees >5 cm in dbh both for urban forests and reference areas are shown here. Shrubs in urban forests mean the cover of shrubs and tree saplings >50 cm in height and <5 cm in dbh. Shrubs in reference areas mean the cover of forest under growth markedly lower than upper canopy layers, i.e. shrubs and young trees (Finnish Forest Research Institute, unpublished data).

T-test or Mann–Whitney test were used in comparing urban and reference forests. Statistically significant differences ($p < 0.05$) are indicated with boldface characters

Kellomäki and Wuorenrinne (1979) found a negative correlation between deterioration of vegetation and size of forest area in urban forests of Espoo in Finland. Furthermore, Guirado et al. (2006) found that vegetation was most worn out at forest edges where recreational use was most active. However, in our study, neither the distance from forest edge nor forest size was correlated with the wear of understorey vegetation. It is not easy to predict behavior of recreationists. Some patches attract more people and others are passed by. Most actively used patches are easy to access and they are often used as shortcuts. There are also worn-out areas in larger forests with constructed paths for recreational activities. In Finland, there are only few restrictions on the use of urban forests for recreational purposes. Thus, people often move off the ‘official’ paths especially if the paths are poorly managed (see Hammitt and Cole 1998). However, a well-designed and managed path network could efficiently concentrate the use of urban forest on paths.

Understorey species composition

The relative proportion of field layer cover increased in urban forests because of the susceptibility of ground layer species to anthropogenic disturbances, mainly trampling (see also Kellomäki and Saastamoinen 1975, Nylund et al. 1979, Hammitt and Cole 1998, Malmivaara et al. 2002). In our study, especially in VT, the cover of herbs increased and the cover of dwarf shrubs, mosses and lichens decreased. In addition to prolonged effects of recreational use (wear and tear of vegetation, shift in species composition towards more trampling tolerant vegetation), this may indicate eutrophication of urban forests.

Recreational use of urban forests also causes changes in soil chemistry. In MT urban forests both soil pH and base saturation has been found to be higher on paths than in untrampled areas (Malmivaara-Lämsä and Fritze 2003, Malmivaara-Lämsä et al., submitted). Walking a dog is a common activity in urban forests, and dogs' faeces provide an extra nutrient load in urban areas (Vehma et al., unpublished results). In addition, nearby residents use urban forests as dumping grounds for garden waste, which may increase soil nutrient levels locally and cause direct floristic changes by introducing species originating outside the forest, garden escapes etc.

Mosses and dwarf shrubs are sensitive to trampling

In general, the trampling tolerance of mosses and particularly lichens is known to be low (Kellomäki and Saastamoinen 1975, Nylund et al. 1979, Florgård 2000, Hamberg et al. 2008). We found that the species *Dicranum polysetum*, *Hylocomium splendens*, and *Pleurozium schreberi* had decreased in urban forests probably due to their sensitivity to trampling, which is in accordance with results of previous studies (Kellomäki and Saastamoinen 1975, Nylund et al. 1979). *H. splendens* has been found to be especially sensitive to trampling. It recovers slowly after disturbance because it probably lacks a soil-buried propagule bank (Jonsson 1993). Furthermore, *H. splendens* is highly sensitive to changes in microclimate, especially to lowered availability of moisture (Busby et al. 1978, Callaghan et al. 1978). Trampling and formation of paths cause changes in forest floor microclimate. Paths and their surroundings are usually drier and warmer than areas of intact vegetation (Liddle 1997). Thus, microclimate in highly trampled urban forest may be suboptimal for *H. splendens* and probably also for other moss species.

In the field layer, the cover of sensitive dwarf shrubs, especially the ever-green *Vaccinium vitis-idaea*, had decreased in urban forests studied. Although the trampling resistance of *V. vitis-idaea* may be better than that of other dwarf shrub species because of its morphology (see Nylund et al. 1979), it is not as resilient as *Vaccinium myrtillus* in the long term. Our results are consistent with the results of Tolvanen et al. (2001) who showed that *V. myrtillus* is generally more resilient and regenerates faster than *V. vitis-idaea* following damage due to its higher growth rate (see also Tolvanen and Laine 1997). In general, dwarf shrubs are sensitive because their regenerative buds are located above ground (see Cole 1995, Liddle 1997), and they regenerate relatively slowly after disturbance. Vegetative regrowth after disturbance takes several years (Rydgren et al. 1998, Hautala et al. 2001), which makes recovery almost impossible in frequently trampled areas.

Successful urban plant species

In our study, small tree saplings (< 50 cm in height), especially *Sorbus aucuparia* but also *Picea abies* in OMT, may have benefited from the free growing space created by moderate trampling (see also Hamberg et al. 2008). The openings established in the ground layer may enhance the regeneration of tree saplings from seeds (Kuuluvainen 1994, Rydgren et al. 1998). In addition, trampling, cutting and the removal of saplings may increase vegetative growth of *S. aucuparia* from root suckers (see Kullman 1986, Zerbe 2001). Also Lehvävirta and Rita (2002) showed that anthropogenic disturbance had positive effects on regeneration of aspen, birch and rowan saplings in urban forests.

Our study shows that *Pteridium aquilinum* and *Melampyrum pratense* thrive in urban forests. They both seem to be resilient species. In their trampling experiment Littlemore and Barker (2003) found that although *P. aquilinum* was least resistant to trampling it was able

to recover well from heavy levels of trampling by the following year. Lehtilä and Syrjänen (1995) have shown that *M. pratense* has a good ability to recover from damage by compensatory growth. According to our results, *Trientalis europaea* had increased in urban MT forests. It may benefit from free growing space created by trampling in the field and ground layer vegetation because its clonal in-growth after disturbance is fast (Hiirsalmi 1969, Rydgren et al. 1998).

In our study, the pioneer moss species *Pohlia nutans* had increased in urban forests. It colonizes bare humus after trampling disturbance by germinating from a soil-buried propagule bank (Jonsson 1993, Koponen 1994, Rydgren et al. 1998).

Other anthropogenic factors affecting understorey vegetation

Another explanation for the low cover of mosses in our study is fragmentation, which increases the proportion of edge zone in urban forests. Although sample plots from 25 m onwards from the forest edge were used in the analyses of vegetation composition it is still possible that edge effects have some influence on our results (Hamberg et al. 2008). Forest edges receive more light and are warmer and drier than forest interiors (Chen et al. 1993). Thus, in our urban areas forest edges are characterized by an abundance of broad-leaved trees, grasses and herbs, which increase the amount of leaf litter on the ground (Lehvävirta and Rita 2002, Malmivaara-Lämsä and Fritze 2003, Hamberg et al. 2008). Mosses tend to withdraw from such areas with dry microclimate and an abundance of litter (Lahti and Väisänen 1987). Also Huggard and Vyse (2002) concluded that mosses may dry out at forest edges because light and temperature conditions are too severe. Thus, moss cover might decrease in small urban forest fragments with a large proportion of edge zone, as was observed in our study.

As broad-leaved trees, grasses and herbs are abundant at forest edges, their litter increases soil nutrient levels there (Mikola 1985, Malmivaara-Lämsä et al., submitted). In addition, forest edges act as concentrators of airborne pollutants and nutrients, e.g. nitrogen (Bobbink et al. 1998, Weathers et al. 2001). Nitrogen load increases soil fertility and causes decrease especially in the share of bryophytes and lichens but also in the share of dwarf shrubs, and increase in the share of herbs and grasses in forest vegetation (Kuusipalo 1996).

The low cover of *Pleurozium schreberi* and *Hylocomium splendens* in urban forests studied may partly be due to nitrogen load and acid deposition in the area (Dirkse and Martakis 1992, Mäkipää 2000a, b). On the contrary, *Brachythecium oedipodium*, which increased in urban forests studied, may have benefited from increased amounts of litter (Mäkipää 2000c, Hamberg et al. 2008) and increased amounts of nitrogen near the forest edges (see Dirkse and Martakis 1992). Light demanding *Pteridium aquilinum* and *Melampyrum pratense* were abundant in urban forests studied. This may be partly due to the abundance of broad-leaved trees and open canopy structure in small forest fragments and in the proximity of forest edges (Tonteri 2000).

Effects of tree layer characteristics on the understorey vegetation

The upper canopy layers of urban forests in our study were more open than in reference forests probably because forest management in urban areas does not have as a goal high production of timber (see Gundersen et al. 2005), in contrast to the reference areas where most of the forests are managed as commercial forests. Recreational users also prefer open, clean and safe-looking forests (Tyrväinen et al. 2003), which influences forest management in urban areas.

In our study, small broad-leaved trees (> 50 cm in height and < 5 cm in dbh) had increased in cover in urban forests. They may have benefited from: 1) fragmentation, which increases the proportion of edge zone with plenty of light and nutrients, 2) eutrophication of urban forests (caused by urban load, dogs' faeces and garden waste, discussed above), 3) lack of large herbivores (i.e. moose, which mainly browse *Sorbus aucuparia*, *Populus tremula* and *Salix caprea* saplings (Andren and Angelstam 1993)), and 4) forest management practices (i.e. thinning, which creates more open and less shady forests and/or undergrowth cuttings, which increase vegetative growth of *Sorbus aucuparia* (see Kullman 1986, Zerbe 2001)). As a result, urban forests are changing towards more open and broad-leaved tree dominated environments.

Tree stand characteristics, such as tree density and ratio of conifers to broad-leaved trees, strongly affect understorey vegetation composition (Kuusipalo 1983, 1985, Mikola 1985, Lahti and Väisänen 1987). In our study, the percentage of broad-leaved trees was a good predictor of total understorey vegetation cover. The cover increased with increasing percentage of broad-leaved trees, which is consistent with previous studies (Mikola 1985, Lahti and Väisänen 1987). Under broad-leaved trees (e.g. *Betula pendula* and *B. pubescens*) soil fertility is higher and, light and temperature conditions are more optimal for fast-growing and light-demanding herb and grass species, which increase in cover (Mikola 1985). In our study, the cover of litter, which increased with increasing amount of broad-leaved trees (see Fig. 1), was also an important determinant of understorey vegetation. The cover of mosses decreases with increasing amounts of litter (see Mikola 1985, Lahti and Väisänen 1987, Hamberg et al. 2008; discussed above).

Conclusions

In our study, site fertility did affect trampling tolerance of urban forests, and the sub-xeric forest type lowest in fertility had the lowest trampling tolerance of the three studied forest types. Based on these results, some management guidelines can be given. We recommend promoting the recreational use of the more durable herb-rich forest type by e.g. constructing paths (giving special emphasis to path maintenance) so that they guide the use on these sites. Furthermore, the sub-xeric forest type should be protected by restricting recreational use of these sites that are particularly sensitive to trampling. For example, natural barriers, like fallen logs and thickets of shrubs and small trees, can be used to restrict trampling in sensitive areas (see Lehvävirta 1999). However, the larger the number of residents around a forest patch the more deteriorated the understorey vegetation will be irrespective of site fertility. Thus, the number of forests left within and at the outskirts of cities should be large enough and sites should be managed, as mentioned above, to ameliorate the effects of recreational use.

The greatest change in the understorey vegetation of all urban forest types studied was the decrease in the cover of ground layer vegetation, which proved to be more sensitive to trampling, and possibly to other anthropogenic disturbances (fragmentation, urban load) than field layer vegetation. Due to trampling, resilient herb species are replacing sensitive dwarf shrubs, and mosses and lichens in urban forests. Increasing fertility in urban areas may lead to more uniform vegetation irrespective of original site fertility (see Kuusipalo 1996). Site types of lowest fertility are likely to change towards more fertile ones, and thus, sub-xeric VT vegetation may disappear from urban areas in the long-run. This development will negatively affect biodiversity and amenity values of urban forests, and thus, lessen the quality of recreational experiences they offer.

Acknowledgements We thank Eeva Karjalainen for her constructive comments on the manuscript. The study received financial support from the Finnish Biodiversity Research Programme (FIBRE, project 48010) and from Maj and Tor Nessling Foundation.

References

- Ahti T, Hämet-Ahti L, Jalas J (1968) Vegetation zones and their sections in northwestern Europe. *Ann Bot Fenn* 5:169–211
- Andren H, Angelstam P (1993) Moose browsing on Scots Pine in relation to stand size and distance to forest edge. *J Appl Ecol* 30(1):133–142
- Amberger A (2006) Recreation use of urban forests: An inter-area comparison. *Urban Forestry and Urban Greening* 4:135–144
- Bobbink R, Hornung M, Roelofs JGM (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J Ecol* 86:717–738
- Busby JR, Bliss LC, Hamilton CD (1978) Microclimate control of growth rate and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecol Monogr* 48:95–110
- Cajander AK (1926) The theory of forest types. *Acta For Fenn* 29(3):108 pp
- Callaghan TV, Collins NJ, Callaghan CH (1978) Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. *Oikos* 31:73–88
- Chen J, Franklin JF, Spies TA (1993) Contrasting microclimates among clearcut, edge and interior of old-growth Douglas-fir forest. *Agric For Meteorol* 63:219–237
- Cole DN (1987) Effects of three seasons of experimental trampling on five montane forest communities and a grassland in Western Montana, USA. *Biol Conserv* 40:219–244
- Cole DN (1995) Experimental trampling of vegetation. II. Predictors of resistance and resilience. *J Veg Sci* 32(1):215–224
- Cole DN, Bayfield NG (1993) Recreational trampling of vegetation: standard experimental procedures. *Biol Conserv* 63:209–215
- Dirkse GM, Martakis GFP (1992) Effects of fertilizer on bryophytes in Swedish experiments on forest fertilization. *Biol Conserv* 59:155–161
- Florgård C (2000) Long-term changes in indigenous vegetation preserved in urban areas. *Landscape Urban Planning* 52:101–116
- Florgård C, Forsberg O (2006) Residents' use of remnant natural vegetation in the residential area of Järvafältet, Stockholm. *Urban Forestry and Urban Greening* 5(2):83–92
- Guirado M, Pino J, Rodà F (2006) Understorey plant species richness and composition in metropolitan forest archipelagos: effects of forest size, adjacent land use and distance to the edge. *Global Ecol Biogeogr* 15:50–62
- Gundersen V, Frivold LH, Löfström I, Jørgensen BB, Falck J, Øyen B-H (2005) Urban woodland management – the case of 13 major Nordic cities. *Urban Forestry and Urban Greening* 3:189–202
- Hamberg L, Lehvävirta S, Malmivaara-Lämsä M, Rita H, Kotze DJ (2008) The effects of habitat edges and trampling on understorey vegetation in urban forests in Helsinki, Finland. *Appl Veg Sci* (in press)
- Hammitt WE, Cole DN (1998) *Wildland recreation: ecology and management*. John Wiley and Sons, New York, 361 pp
- Hautala H, Tolvanen A, Nuortila C (2001) Regeneration strategies of dominant boreal forest dwarf shrubs in response to selective removal of understorey layers. *J Veg Sci* 12:503–510
- Hämet-Ahti L, Suominen J, Ulvinen T, Uotila P (eds) (1998) *Retkeilykasvio* [Field flora of Finland]. Finnish Museum of Natural History, Botanical Museum, Helsinki
- Hiirsalmi H (1969) *Trientalis europaea* L.: a study of the reproductive biology, ecology and variation in Finland. *Ann Bot Fenn* 6:119–173
- Huggard DJ, Vyse A (2002) Edge effects in high-elevation forests at Sicomous Creek. *Silviculture*. Extension note 62, 1–8. Ministry of Forests, Forest Science Program, British Columbia
- Jatinen E (1973) Recreational use of Helsinki's forests. *Folia For* 186
- Jonsson BG (1993) The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. *J Veg Sci* 4:819–826
- Kellomäki S (1973) Ground cover response to trampling in a spruce stand of *Myrtillus* type (in Finnish with English summary). *Silva Fenn* 7(2):96–113
- Kellomäki S (1977) Deterioration of forest ground cover during trampling. *Silva Fenn* 11(3):153–161
- Kellomäki S, Saastamoinen V-L (1975) Trampling tolerance of forest vegetation. *Acta For Fenn* 147:1–22
- Kellomäki S, Wuorenrinne H (1979) On factors effecting on deterioration of urban forests (in Finnish with English summary). *Silva Fenn* 13(2):177–183

- Koponen T (1994) *Lehtisammalten määrittäysopas* [Moss identification guide]. Helsingin yliopiston kasvitieteen laitoksen monisteita 139, Helsinki
- Kullman L (1986) Temporal and spatial aspects of subalpine populations of *Sorbus aucuparia* in Sweden. *Ann Bot Fenn* 23:267–275
- Kuuluvainen T (1994) Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Ann Zool Fenn* 31:35–51
- Kuusipalo J (1983) Distribution of vegetation on mesic forest sites in relation to some characteristics of the tree stand and soil fertility. *Silva Fenn* 17(4):403–418
- Kuusipalo J (1985) An ecological study of upland forest site classification in southern Finland. *Acta For Fenn* 192:1–77
- Kuusipalo J (1996) Suomen metsätyypit [Forest site types of Finland]. Kirjayhtymä, Helsinki
- Lahti T, Väisänen RA (1987) Ecological gradients of boreal forests in South Finland: an ordination test of Cajander's forest site type theory. *Vegetatio* 68:145–156
- Lehtilä K, Syrjänen K (1995) Compensatory responses of two *Melampyrum* species after damage. *Funct Ecol* 9:511–517
- Lehvävirta S (1999) Structural elements as barriers against wear in urban woodlands. *Urban Ecosyst* 3:45–56
- Lehvävirta S, Rita H (2002) Natural regeneration of trees in urban woodlands. *J Veg Sci* 13:57–66
- Liddle MJ (1975) A theoretical relationship between the primary productivity of vegetation and its ability to tolerate trampling. *Biol Conserv* 8:251–255
- Liddle MJ (1997) *Recreation ecology: The ecological impact of outdoor recreation and ecotourism*. Chapman & Hall, London
- Littlemore J, Barker S (2003) The ecological response of forest ground flora and soils to experimental trampling in British urban woodlands. *Urban Ecosyst* 5:257–276
- Malmivaara-Lämsä M, Fritze H (2003) Effects of wear and above ground forest site type characteristics on the soil microbial community structure in an urban setting. *Plant Soil* 256:187–203
- Malmivaara M, Löfström I, Vanha-Majamaa I (2002) Anthropogenic effects on understorey vegetation in Myrtillus type urban forests in southern Finland. *Silva Fenn* 36(1):367–381
- Mäkipää R (2000a) *Pleurozium schreberi*. In: Reinikainen A, Mäkipää R, Vanha-Majamaa I, Hotanen J-P (eds) *Kasvit muuttuvassa metsäluonossa* [Changes in the frequency and abundance of forest and mire plants in Finland since 1950], Tammi, Helsinki, pp 251–253
- Mäkipää R (2000b) *Hylocomium splendens*. In: Reinikainen A, Mäkipää R, Vanha-Majamaa I, Hotanen J-P (eds) *Kasvit muuttuvassa metsäluonossa* [Changes in the frequency and abundance of forest and mire plants in Finland since 1950], Tammi, Helsinki, pp 248–250
- Mäkipää R (2000c) *Brachythecium*-suku. In: Reinikainen A, Mäkipää R, Vanha-Majamaa I, Hotanen J-P (eds) *Kasvit muuttuvassa metsäluonossa* [Changes in the frequency and abundance of forest and mire plants in Finland since 1950], Tammi, Helsinki, pp 238–239
- Mikola P (1985) The effect of tree species on the biological properties of forest soil. National Swedish Environmental Protection Board, Rapport 3017, 27 pp
- Nylund M, Nylund L, Kellomäki S, Haapanen A (1979) Deterioration of forest ground vegetation and decrease of radial growth of trees on camping sites. *Silva Fenn* 13(4):343–356
- R Development Core Team (2005) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Roovers P, Verheyen K, Hermy M, Gulinck H (2004) Experimental trampling and vegetation recovery in some common forest and heath communities. *Appl Veg Sci* 7:111–118
- Rydgren K, Hestmark G, Økland R (1998) Revegetation following experimental disturbance in a boreal old-growth *Picea abies* forest. *J Veg Sci* 9:763–776
- Sievänen T (1987) Experiences of forest recreation in another culture: A comparison between Finland and Minnesota. *Scand For Econ* 29:49–56
- Thimonier A, Dupouey JL, Timbal J (1992) Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine Plain under the influence of atmospheric deposition. *For Ecol Manag* 55:149–167
- Tolvanen A, Laine K (1997) Effects of reproduction and artificial herbivory on vegetative growth and resource levels in deciduous and evergreen dwarf shrubs. *Can J Bot* 75:656–666
- Tolvanen A, Forbes B, Rytönen K, Laine K (2001) Regeneration of dominant plants after short-term pedestrian trampling in subarctic plant communities. In: FE Wielgolaski (ed) *Nordic mountain birch ecosystems*, pp 359–368. Man and the Biosphere Series Volume 27, UNESCO, Paris, and Parthenon Publishing, Carnforth
- Tonteri T (2000) *Melampyrum pratense*. In: Reinikainen A, Mäkipää R, Vanha-Majamaa I, Hotanen J-P (eds) *Kasvit muuttuvassa metsäluonossa* [Changes in the frequency and abundance of forest and mire plants in Finland since 1950], Tammi, Helsinki, pp 202–204
- Tonteri T, Hotanen J-P, Mäkipää R, Nousiainen H, Reinikainen A, Tamminen M (2005) Metsäkasvit kasvupaikoillaan-kasvupaikkatyypin, kasvillisuusvyöhykkeen, puuston kehitysluokan ja puulajin yhteys

- kasvilajien runsaussuhteisiin [Forest plants and forest site types]. Metsäntutkimuslaitoksen tiedonantoja 946:1–106
- Tyrväinen L, Silvennoinen H, Kolehmainen O (2003) Ecological and aesthetic values in urban forest management. *Urban Forestry and Urban Greening* 1:135–149
- Wade TG, Riitters KH, Wickham JD, Jones KB (2003) Distribution and causes of global forest fragmentation. *Conserv Ecol* 7(2):7. [online] URL: <http://www.consecol.org/vol7/iss2/art7/>
- Weathers KC, Cadenasso ML, Pickett STA (2001) Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conserv Biol* 15:1506–1514
- Zerbe S (2001) On the ecology of *Sorbus aucuparia* (Rosaceae) with special regard to germination, establishment and growth. *Polish Bot J* 46:229–239